Saccades and microsaccades during visual fixation, exploration, and search: Foundations for a common saccadic generator

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Microsaccades are known to occur during prolonged visual fixation, but it is a matter of controversy whether they also happen during free-viewing. Here we set out to determine: 1) whether microsaccades occur during free visual exploration and visual search, 2) whether microsaccade dynamics vary as a function of visual stimulation and viewing task, and 3) whether saccades and microsaccades share characteristics that might argue in favor of a common saccade–microsaccade oculomotor generator. Human subjects viewed naturalistic stimuli while performing various viewing tasks, including visual exploration, visual search, and prolonged visual fixation. Their eye movements were simultaneously recorded with high precision. Our results show that microsaccades are produced during the fixation periods that occur during visual exploration and visual search. Microsaccade dynamics during free-viewing moreover varied as a function of visual stimulation and viewing task, with increasingly demanding tasks resulting in increased microsaccade production. Moreover, saccades and microsaccades had comparable spatiotemporal characteristics, including the presence of equivalent refractory periods between all pair-wise combinations of saccades and microsaccades. Thus our results indicate a microsaccade–saccade continuum and support the hypothesis of a common oculomotor generator for saccades and microsaccades.

Keywords: drifts, fixational eye movements, free-viewing, intersaccadic intervals, natural scenes, oculomotor control

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Introduction

Visual exploration and visual search are characterized by the alternation of *saccades* and *fixation* periods. However, fixation periods are defined arbitrarily because the eyes are never completely still (Ditchburn & Ginsborg, 1952, 1953; Martinez-Conde, Macknik, & Hubel, 2004; Ratliff & Riggs, 1950; Riggs & Ratliff, 1952; Yarbus, 1967). Fixational eye movements include tremor, drifts, and microsaccades, i.e., small involuntary saccades that occur during fixation. But microsaccades cannot be differentiated from saccades according to their magnitude alone, as exploratory or voluntary saccades can be the same size as microsaccades. Indeed, it is not possible to differentiate saccades from microsaccades according to any physical characteristic. For this reason, one cannot know whether a small-sized saccade constitutes a fixational microsaccade (and thus it is part of a fixation period), or an exploratory, non-fixational saccade.

Much work has been done to address the descriptive parameters of saccades and microsaccades; see Martinez-Conde et al. (2004) and Martinez-Conde & Macknik (2008) for reviews of microsaccade characteristics. However, little is known about the timing of microsaccades, and its interplay with the timing of saccades. Here we explore the spatiotemporal interactions of saccades and microsaccades during the presentation of naturalistic stimuli in visual exploration, visual search, and prolonged visual fixation. If microsaccades and saccades share both their spatial and temporal dynamics, it would support the notion that saccades and microsaccades share a common oculomotor basis.

Mounting evidence points toward a unified neural generator of saccades and microsaccades. Zuber and Stark (1965) originally found that microsaccades lie on the saccadic main sequence. Saccades and microsaccades are

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generally binocular and conjugate (Ditchburn & Ginsborg, 1953; Lord, 1951; Yarbus, 1967), and both saccades and microsaccades are correlated to shifts in spatial attention (Engbert, 2006; Engbert & Kliegl, 2003b; Rolfs, Engbert, & Kliegl, 2004, 2005). Rolfs, Laubrock, and Kliegl (2006) recently examined the latency of voluntary saccades directed to a peripheral target as a function of preceding microsaccade rate. They found that saccadic latency increased if microsaccades occurred up to 300 ms before the saccadic 'go signal'. In a subsequent paper, Rolfs, Kliegl, and Engbert (2008) proposed that microsaccades may be generated in a motor map commonly coding for microsaccades and saccades in the superior colliculus.

Here we build on these results by determining the precise refractory periods between all pair-wise combinations of microsaccades and saccades as a function of viewing condition and task. Our results show that saccades and microsaccades have comparable spatiotemporal characteristics in all visual tasks and viewing conditions tested, thus supporting the common generator hypothesis.

Methods

Subjects

Eight subjects (6 females, 2 males) with normal or corrected-to-normal vision participated in this study. Each subject participated in 3 experimental sessions, of ~60 minutes each. Seven of the subjects were naïve (they were paid $15/session). Experiments were carried out under the guidelines of the Barrow Neurological Institute's Institutional Review Board (protocol number 04BN039) and written informed consent was obtained from each participant.

Experimental design

Subjects rested their head on a chin-rest, 57 cm from a linearized video monitor (Barco Reference Calibrator V, 75 Hz refresh rate). Eye position was acquired non-invasively with a fast video-based eye movement monitor (EyeLink II, SR Research, Ontario, Canada). The EyeLink II system records fixational eye movements simultaneously in both eyes (temporal resolution 500 samples/s; instrument noise 0.01 deg RMS), in its off-the-shelf configuration. We identified saccades and microsaccades automatically with an objective algorithm (see Engbert & Kliegl, 2003b, for details). Equivalent results were obtained with a different algorithm (Martinez-Conde, 2006; Martinez-Conde & Macknik, 2007; Martinez-Conde, Macknik, & Hubel, 2000, 2002; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006; data not shown). To reduce the amount of potential noise (Engbert, 2006), we considered only binocular saccades/microsaccades, that is, saccades/microsaccades that occurred simultaneously in both eyes during at least one data sample (2 ms) (Engbert, 2006; Engbert & Mergenthaler, 2006; Laubrock, Engbert, & Kliegl, 2005; Rolfs et al., 2006; Troncoso, Macknik, & Martinez-Conde, 2008; Troncoso, Macknik, Otero-Millan, & Martinez-Conde, 2008). Additionally, we imposed a minimum intersaccadic interval of 20 ms so that potential overshoot corrections might not be categorized as new saccades/microsaccades (Møller, Laursen, Tygesen, & Sjølie, 2002; Troncoso, Macknik, & Martinez-Conde, 2008).

We tested 8 experimental conditions (4 fixation conditions and 4 free-viewing conditions). In the fixation conditions, subjects had to fixate a red cross (0.75 degrees wide) on the center of the screen, within a 2 deg × 2 deg window. This window size produced loose fixation, typical of natural fixation behavior (Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002, 2004). The subject received auditory feedback (a short beep) whenever his/her gaze left the fixation window for more than 500 ms (<500 ms gaze excursions were permitted to allow for blinks). In the free-viewing conditions, subjects were free to move their eyes over the visual scene. No fixation cross was presented, and the auditory alert was only played if the subject's gaze left the area of the image for more than 500 ms. Eye movements exceeding the fixation window/image area were also recorded.

We presented 15 different visual scenes per condition (except for the blank conditions, see below). As there were 8 conditions, this resulted in a total of 120 trials. The experiment was conducted over 3 sessions of 40 trials each. Each visual scene was one of the following:

a. Blank scene,
b. Natural scene,
c. "Picture puzzle", or
d. "Where's Waldo" scene.

The scenes presented in conditions b and c were scanned from the *LIFE Picture Puzzle* books (Adams, 2006a, 2006b, 2006c). The scenes presented in condition d were scanned from the *Where's Waldo* books (Handford, 2007a, 2007b, 2007c). All images were equalized for average luminance and RMS contrast (except for the blank scene, which was 50% gray). All images had the same size (36 deg (w) × 25.2 deg (h)) and were centered on the monitor screen. The size and resolution of the objects depicted in the images were such that subjects could perform all tasks comfortably. The visual scenes presented in the fixation and free-viewing conditions were identical, except for the presence/absence of the fixation cross.

In the fixation conditions, the subject's task (i.e., prolonged fixation) did not vary: only the visual scene changed. In the free-viewing conditions, the subject's task varied according to the visual scene presented (Figure 1).

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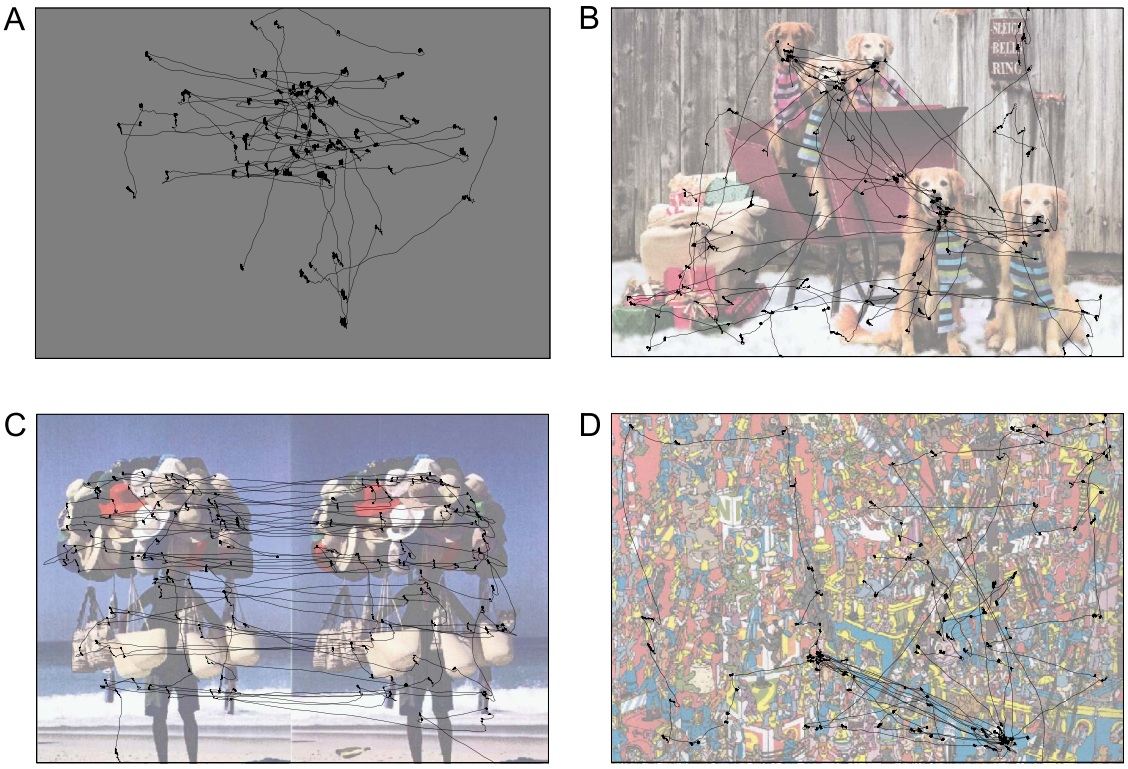

Figure 1. Monocular eye-position traces (45 s each) during typical free-viewing trials. Different strategies can be observed for different combinations of visual stimuli and viewing task. The visual images are reproduced in low contrast, for clarity. (A) Visual exploration of a blank (50% gray) scene is sluggish and uneven. The subject's gaze tends to remain near the center of the screen. (B) Visual exploration of a natural scene. Eye fixations concentrate on salient parts of the image (such as faces vs. non-faces, and foreground vs. background). (C) Picture puzzle visual search. Large horizontal saccades are predominant, linking equivalent points in the two images. (D) Where's Waldo search task. Higher concentrations of fixations can be observed over the two identified targets ("Waldo" and "Wenda" characters). See also Supplementary Movies 1–4.

Conditions a and b (blank scene and natural scene) required free visual exploration of the scene (i.e., the subject was instructed to explore the visual scene at will). Conditions c and d involved visual searches. In condition c (Picture puzzles), the subject was presented with two side-by-side near-identical visual scenes and had to find all the differences between them. In condition d (Where's Waldo) the subject had to conduct the classic cartoon visual search task (i.e., the subject had to find Waldo and other relevant characters/objects from the Where's Waldo books).

Conditions were pseudorandomly interleaved. Each trial was preceded by an "instructions" screen that indicated the type of task to be performed. Before the Where's Waldo trials, the instructions screen illustrated the various cartoon characters and objects to be identified. When the subjects pressed the spacebar, the instructions screen disappeared and the trial started. Each trial was 45-s long. At the end of the Picture puzzle and Where's Waldo trials, the subjects were asked to indicate, using the mouse, the screen locations corresponding to the detected objects/differences. In the Picture puzzle condition, subjects were required to indicate the differences on the left image only. Previous to our analyses, we duplicated these reported locations on the corresponding regions of the right image. Table 2 indicates various parameters of fixations and microsaccades near identified targets. Such regions of interest were defined as the area under a 2 × 2 deg window centered on each reported location (and its "mirror" area in the Picture puzzle condition). This method worked very well to identify the regions of interest in the Where's Waldo condition, but it had some potential caveats in the identification of regions of interest in the Picture puzzles. Specifically, the location of the 2 × 2 deg window over the Picture puzzle images may not have always corresponded to a region of interest. For instance, if a visual object was larger/longer in one image than in the other, the location clicked by the subject may not have been the specific region fixated by the subject when he/she spotted the difference. Further, if the difference between the two images consisted on two different locations of an identical object, mirroring the location of the left-image click over the right image would not have been an optimal method to identify the right-image region of interest. These issues may have led us to underestimate the strength of the effects (i.e., the various microsaccade and fixation parameters near identified targets summarized in Table 2) in the Picture puzzle vs. the Where's Waldo

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	Fixation				Free-viewing			
	Blank scene	Natural scene	Picture puzzle	Where's Waldo	Blank scene	Natural scene	Picture puzzle	Where's Waldo
All saccades								
Rate (N/sec)	0.8 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	0.8 ± 0.1	1.7 ± 0.2	2.9 ± 0.2	3.5 ± 0.2	3.3 ± 0.1
Magnitude (deg)	0.43 ± 0.05	0.53 ± 0.08	0.6 ± 0.1	0.46 ± 0.06	7 ± 1	4.5 ± 0.4	6.8 ± 0.3	3.6 ± 0.2
Duration (ms)	12.6 ± 0.1	13.2 ± 1.1	13.0 ± 1.2	12.5 ± 0.9	42 ± 3	30 ± 2	33.5 ± 0.9	28 ± 1
Peak vel. (deg/s)	42 ± 4	48 ± 5	48 ± 6	43 ± 4	220 ± 20	202 ± 8	257 ± 8	184 ± 5
Saccades ≤ 3 deg								
Rate (N/sec)	0.8 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.6 ± 0.1	1.4 ± 0.1	1.6 ± 0.1	1.8 ± 0.1
Magnitude (deg)	0.41 ± 0.04	0.44 ± 0.04	0.43 ± 0.05	0.42 ± 0.04	1.52 ± 0.06	1.38 ± 0.03	1.52 ± 0.03	1.45 ± 0.03
Duration (ms)	13 ± 1	13 ± 1	12 ± 1	12 ± 1	24 ± 1	19 ± 1	19 ± 1	20 ± 1
Peak vel. (deg/s)	42 ± 3	44 ± 3	43 ± 4	41 ± 3	98 ± 5	102 ± 3	117 ± 4	108 ± 3

Table 1. Saccade parameters (rate, magnitude, duration, peak velocity) in each experimental condition. *Top*: All saccades (see also Figure 2A). *Bottom*: Saccades smaller than 3 deg (see also Figure 2B). All saccade rates were calculated taken into consideration the total time in each trial. Means and standard errors were calculated from the mean values for each subject (N = 8 subjects).

conditions. Thus the Picture puzzle microsaccade and fixation parameters near identified targets indicated in Table 2 must be considered a conservative estimate. It is possible that more refined methods to identify the regions of interest in the Where's Waldo and Picture puzzle conditions would have lead to closer (or even equivalent) microsaccade and fixation parameters in both types of trials. Future research will explore this possibility.

Calculation of microsaccade and saccade parameters

Average fixation durations and saccade/microsaccade magnitudes, durations, and peak velocities were first calculated for each subject and each trial separately. Then, all trials in each condition were averaged. Finally, averages and standard errors were calculated across subjects. Microsaccade rates during free-viewing were calculated taking into account only the time spent in fixation periods: the total number of microsaccades in each subject and trial was divided by the total time spent in fixation during that trial. We then averaged all the trials for each condition, and calculated the averages and standard errors across subjects (Figures 3 and 6, Tables 1 and 2).

Intersaccadic interval distribution fitting

For the analyses in Figures 7 and 8 we fitted the intersaccadic interval distributions using an ex-Gaussian

	Blank scene	Natural scene	Picture puzzle	Where's Waldo
Microsaccade rate (N/sec)	0.2 ± 0.1	0.6 ± 0.1	0.5 ± 0.1	0.6 ± 0.1
Microsaccade rate near identified targets (N/sec)	–	–	0.6 ± 0.1	1.3 ± 0.1
% of fixations with microsaccades	7 ± 2	14 ± 1	10 ± 1	15 ± 2
% of fixations near identified targets with microsaccades	–	–	15 ± 2	45 ± 5
Avg. fixation duration (ms)	470 ± 50	300 ± 10	234 ± 7	283 ± 4
Avg. fixation duration near identified targets (ms)	–	–	255 ± 7	600 ± 90
Avg. microsaccade magnitude (deg)	0.55 ± 0.03	0.58 ± 0.01	0.63 ± 0.01	0.60 ± 0.01
Avg. microsaccade magnitude near identified targets (deg)	–	–	0.64 ± 0.01	0.53 ± 0.01
% Time spent in fixation	79 ± 2	80 ± 2	77 ± 3	83 ± 2

Table 2. Microsaccade dynamics in the fixation periods during free-viewing. Microsaccade rates during prolonged fixation and during the fixation periods in free-viewing were comparable, with the exception of the free exploration of a blank scene. Although the blank scene condition had the longest fixation durations, the microsaccade rate was lowest. The Where's Waldo condition had the highest microsaccade rate, the highest percentage of fixations with at least one microsaccade, and the highest average fixation duration near identified targets (600 ms). The percentage of time spent in fixation periods during free-viewing was similar (approximately 80%) in all conditions (blank scene, natural scene, Picture puzzle, and Where's Waldo). To calculate microsaccade rates during free-viewing, we took into account only the time spent in fixation periods. The beginning and end of fixation periods were marked by either two saccades (i.e., non-microsaccades) or by a saccade and a blink. N = 8 subjects.

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function. The ex-Gaussian is the most commonly used function to estimate the distribution of reaction time data (Van Zandt, 2000). An ex-Gaussian random variable is obtained when two random variables—one with a normal distribution and the other with an exponential distribution—are summed. The probability distribution function of an ex-Gaussian random variable is the result of the convolution of a Gaussian and an exponential function. It fits empirical reaction time distributions well (Hockley, 1984; Juhel, 1993; Rohrer & Wixted, 1994). Also, Engbert (2006) previously fit intersaccadic intervals between successive microsaccades with an exponential distribution. To obtain the three parameters of the ex-Gaussian that best fits the data we used a maximum likelihood estimation algorithm.

Results

Subjects either fixated a small cross on the center of the monitor, or freely viewed (i.e., explored/searched) a visual scene. Four types of visual scenes were presented:

a. Blank scene (50% gray);
b. Natural scene;
c. Picture puzzle;
d. Where's Waldo.

Each visual scene was presented twice: once while the subject fixated, and once while the subject freely viewed the images. In the fixation trials, the subjects had to fixated a central cross, irrespective of the background scene. In the free-viewing trials, the subjects' task varied depending on the type of scene presented. In the blank scene and natural scene conditions, the subjects were asked to explore the image at will. In the Picture puzzle condition, the subjects were required to find all the differences between two side-by-side nearly identical images and indicate their locations at the end of the trial, using the computer mouse. In the Where's Waldo condition, the subjects performed the classical cartoon visual search task—i.e., they had to locate various cartoon characters/objects among numerous distracters and indicate the location of identified targets at the end of the trial. Figure 1 and Supplementary Movies 1–4 show representative eye position traces for each of the free-viewing tasks. See Methods section for details.

Saccade and microsaccade dynamics during visual fixation and free-viewing

The dynamics of microsaccades during visual fixation vs. free-viewing have not been previously examined systematically and objectively (but see Martinez-Conde, 2006 for some preliminary observations). Here we asked whether microsaccades are produced during naturalistic visual exploration and visual search, and whether microsaccade dynamics vary as a function of viewing task. Figure 2 plots the main sequences for all saccades/microsaccades in each experimental condition, for all subjects. Figure 2A includes all saccade/microsaccade magnitudes, and Figure 2B displays the same data in higher detail (for saccade/microsaccade magnitudes of less than 3 degrees). Several observations can be drawn:

1. Saccade/microsaccade dynamics are equivalent across all fixation conditions, irrespective of the background image presented (blank scene/natural scene/Picture puzzle/Where's Waldo scene).
2. Saccade/microsaccade dynamics vary considerably across the free-viewing conditions, presumably as a function of the visual scene presented and/or task performed.
3. The dynamics of the smaller saccades (putative microsaccades) are grossly dissimilar for fixation vs. free-viewing of the same images.

Microsaccade characterization during prolonged fixation and during the fixation periods in free-viewing

To address the interplay between saccades and microsaccades during free-viewing, one must first decide which eye movements should be classified as saccades vs. microsaccades. This poses a challenge: because exploratory and/or voluntary saccades can be the same size as microsaccades, one cannot distinguish between saccades and microsaccades based on their magnitude (or any other known physical parameter). Microsaccades can be defined only *operationally*, as *involuntary saccades that are produced while attempting to fixate* (Martinez-Conde, 2006). Thus if the subject is performing a fixation task, most saccades detected will be microsaccades by definition (regular exploratory or reflex saccades may also occur on occasion).

Free-viewing presents the possibility of classifying microsaccades and saccades as a function of the subject's intent: saccades produced during fixation periods can be defined as microsaccades, whereas saccades produced during active exploration can be defined as regular saccades. One obstacle to this strategy is that we are usually not aware of our eye movements: during normal visual exploration/search most saccades are involuntary, regardless of their size. Having the subjects continuously indicate their intent to fixate vs. shift their gaze would add to the difficulty of the task and might result in rather artificial viewing conditions.

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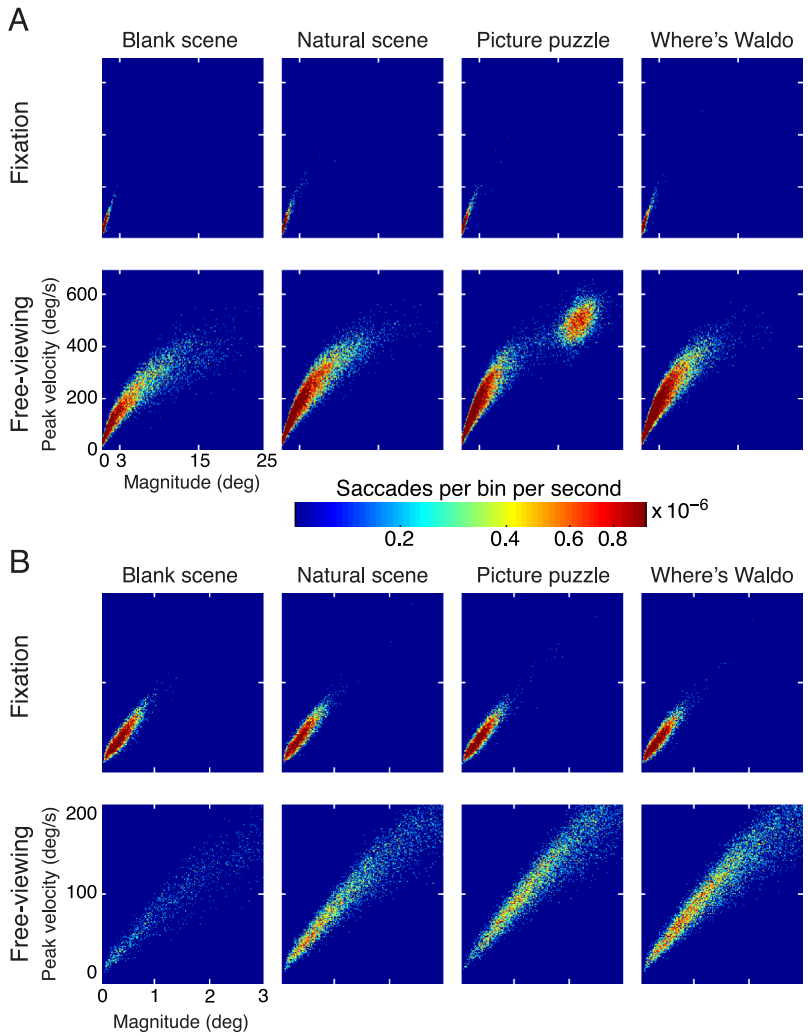

Figure 2. Saccadic main sequences during visual fixation and free-viewing. (A) Main sequences illustrating all saccades. Notice cluster of ~20-deg saccades in the free-viewing Picture puzzle condition (corresponding to horizontal saccades linking equivalent points in the two side-by-side images; see also Figure 1C). (B) Main sequences from (A) in higher detail (saccade/microsaccade magnitudes of less than 3 degrees). Main sequences are equivalent for all the fixation conditions. However, free-viewing of the same images results in very different saccade dynamics. Also, the dynamics of small saccades in the free-viewing conditions appear to vary as a function of stimulus (blank vs. visual scene) and task (free exploration vs. Picture puzzle search vs. Where's Waldo search). Such differences may be partially due to varying cognitive/attentional demands across the free-viewing conditions. N = 8 subjects.

An alternative way to classify microsaccades vs. saccades during free-viewing—without complicating and/or interfering with the subject's task—is to:

1. Establish the physical parameters of saccades produced during prolonged fixation (most of these saccades are *microsaccades* by definition, as stated above), and
2. Use those parameters to identify microsaccades in free-viewing conditions.

Figure 2 plots the magnitude–peak velocity relationship for all saccades produced during prolonged fixation (45-s long trials; see Methods section for details). Regardless of the background scene presented, the vast majority of saccades produced during prolonged fixation had magnitudes below 1 deg. Here we will consider those saccades as microsaccades, in agreement with previous studies (Betta, Galfano, & Turatto, 2007; Betta & Turatto, 2006; Engbert, 2006; Engbert & Kliegl, 2003a, 2003b, 2004; Engbert & Mergenthaler, 2006; Galfano, Betta, & Turatto, 2004; Laubrock et al., 2005; Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002, 2004, 2006; Rolfs et al., 2004, 2006; Troncoso, Macknik, & Martinez-Conde, 2008; Troncoso, Macknik, Otero-Millan, et al., 2008; Turatto, Valsecchi, Tamè, & Betta, 2007; Valsecchi, Betta, & Turatto, 2007; Valsecchi & Turatto, 2007) and while keeping in mind the caveats discussed above. See also Methods section for further details on the saccade/microsaccade detecting algorithm. Now, we may

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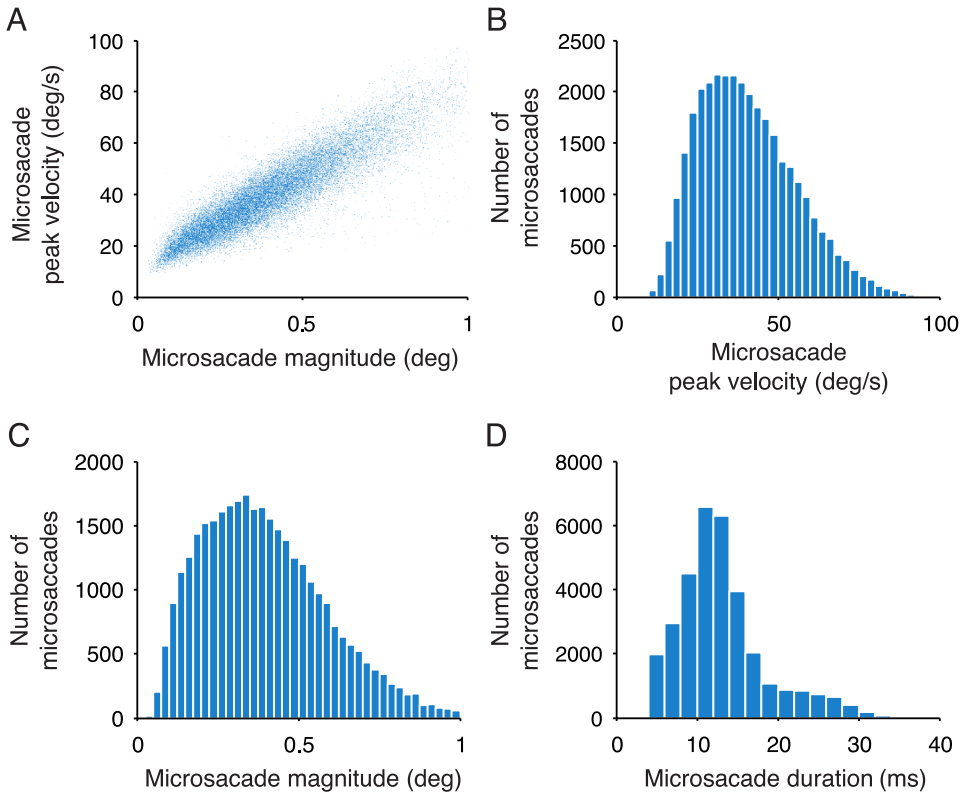

	Blank scene	Natural scene	Picture puzzle	Where's Waldo	Avg.
Rate (N/sec)	0.8 ± 0.1	0.7 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.8 ± 0.1
Magnitude (deg)	0.39 ± 0.03	0.39 ± 0.03	0.37 ± 0.03	0.36 ± 0.03	0.37 ± 0.03
Duration (ms)	12 ± 1	12 ± 1	12 ± 1	12 ± 1	12 ± 1
Peak vel. (deg/s)	39 ± 2	40 ± 2	39 ± 2	38 ± 2	39 ± 2

Figure 3. Microsaccade parameters during prolonged fixation. (A) Microsaccade main sequence (N = 33,230). (B) Microsaccade peak velocity distribution. (C) Distribution of microsaccade magnitudes. (D) Distribution of microsaccade durations. All the fixation conditions have been grouped. The table summarizes various microsaccade dynamics (rate, magnitude, duration, peak velocity) in each experimental condition. Microsaccade rates were calculated taken into consideration the total time in each trial. Means and standard errors were calculated from the mean values for each subject (N = 8 subjects).

apply the same classification to saccades/microsaccades produced during free-viewing. Thus from here on we will refer to saccades smaller than 1 deg as microsaccades, irrespective of whether they were produced during prolonged fixation conditions, or during the brief fixation periods encompassed during the free-viewing conditions. Correspondingly, we will define fixation periods in free-viewing as those periods between saccades larger than 1 deg (or in between a saccade larger than 1 deg and a blink, see Methods section). This procedure has the important advantage that the parameters used to identify microsaccades during free-viewing are derived from the distribution of involuntary saccades during visual fixation (i.e., veritable microsaccades, Figures 2 and 3). However, one must keep in mind that no microsaccade-detecting method can ensure that all putative microsaccades (produced during free-viewing or even during prolonged fixation) are involuntary (as opposed to small voluntary saccades). Conversely, some of the >1 deg saccades produced during prolonged fixation (and possibly during free-viewing) may be involuntary and could be thus categorized as microsaccades. Table 1 summarizes various dynamics of saccades/microsaccades during fixation and free-viewing conditions (corresponding to the main sequences in Figure 2). Figure 3 plots the microsaccadic main sequence and related parameters for the four fixation conditions together.

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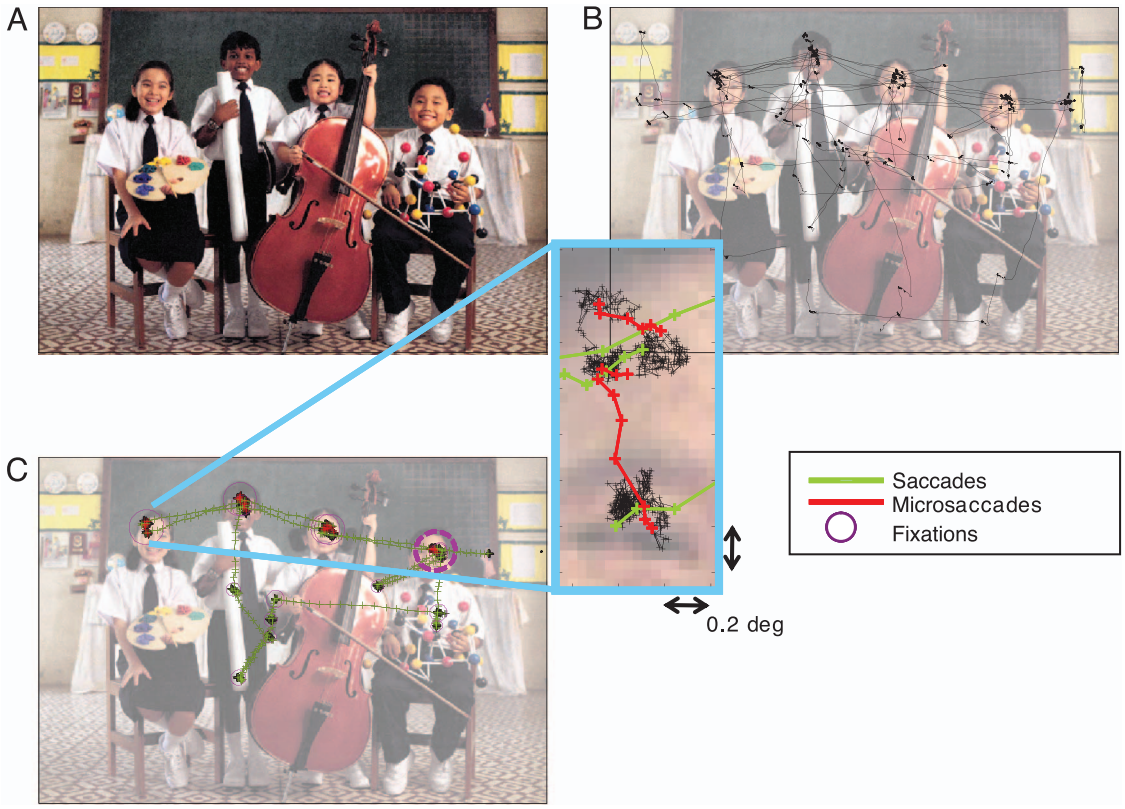

Figure 4. Microsaccades during free-viewing. (A) Image equalized for luminance and RMS contrast. (B) A 45-s monocular eye position trace during free visual exploration, plotted over a low-contrast version of the image (for clarity). (C) A 10-s period from (B). The area of each circle indicates the duration of the fixation period (smaller area circles correspond to fixations of linearly shorter durations). The largest circle (dashed purple line) corresponds to a 1,678 ms fixation period. Human faces attracted long-duration fixations and proved to be a primary focus of microsaccades (red).

Microsaccades during free-viewing were most prevalent at the points of the image that were meaningful for the task. Thus microsaccades tended to occur when foveating human faces and other salient objects during free visual exploration (Figure 4), or on the regions with identified targets during visual search tasks (Picture puzzles and Where's Waldo conditions). See Supplementary Movies 5–6. These observations may be related to the recent proposal that microsaccades significantly "re-sharpen" the image and improve spatial resolution (Donner & Hemilä, 2007).

Figure 5 illustrates the distribution of fixation durations across the free-viewing conditions. The rate and number of microsaccades increased parametrically with fixation duration in all free-viewing conditions (Figures 5C and 5D), with a quasi-linear relationship between number of microsaccades and fixation duration (Figure 5D). The example in Figure 4C illustrates how microsaccades are contained within the fixation periods with longest durations. However, the slope of the curves in Figures 5C and 5D varied across conditions, with the steepest increase for the Where's Waldo condition. Interestingly, visual exploration of a blank scene resulted in the longest fixation durations (Figure 5A), but the lowest number of fixations with microsaccades (Figure 5B), thus suggesting that microsaccades may require the presence of a visual/attentional target to anchor to (see also Table 2). Further, the difference in microsaccade dynamics in the Where's Waldo condition vs. the blank scene exploration condition may result from the varied attentional/cognitive demands of both tasks (highest in the Where's Waldo search task and lowest in the blank scene exploration task). Thus microsaccade production is not solely dependent on fixation duration, but it may also be affected by both visual stimulation (blank vs. natural scene) and the cognitive demands of the task performed.

Table 2 summarizes the occurrence of microsaccades across the free-viewing conditions. Subjects were engaged in fixation during approximately 80% of the free-viewing time, irrespective of experimental condition. During the blank scene exploration, average fixation durations were long (470 ± 50 ms) but average microsaccade rates were lowest (0.2 ± 0.1 Hz). Microsaccade production was highest in the Where's Waldo condition. During the Where's Waldo search, the average microsaccade rate was 0.6 ± 0.1 Hz, and 15 ± 2% of all fixations contained at least one microsaccade. Microsaccade production increased even further when only the regions with identified targets (as indicated by the subject) were considered. In such case, the

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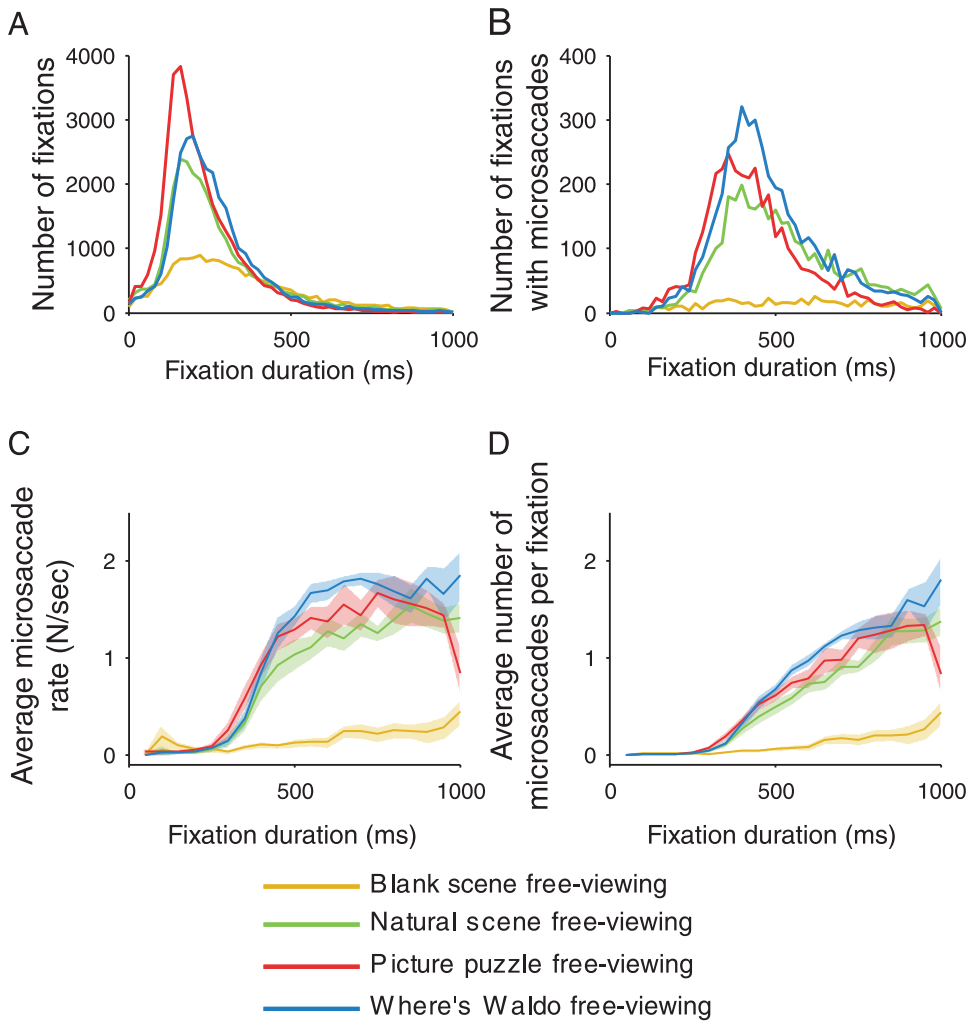

Figure 5. Fixations and microsaccades during free-viewing. (A) Distribution of fixation durations across free-viewing conditions. (B) Distribution of fixation durations, for fixation periods containing at least 1 microsaccade. (C) Microsaccade rate as a function of fixation duration. Microsaccade rate is approximately constant after 400 ms in all conditions. (D) Microsaccade numbers per fixation period, as a function of fixation period duration. The number of microsaccades per fixation period increases linearly after approximately 400 ms. Panels C and D illustrate that microsaccade production does not solely depend on fixation duration, but it is also affected by visual stimulation (blank vs. natural scene) and—to a lesser extent—by the specific free-viewing task performed. N = 8 subjects.

average microsaccade rate escalated to 1.3 ± 0.1 Hz for the Where's Waldo task (a 70% increase with respect to microsaccade rates during prolonged fixation), and about half of the fixation periods (45 ± 5%) contained microsaccades. Moreover, the average duration of fixations in the regions of identified Where's Waldo targets (600 ± 90 ms) surpassed the average fixation duration during free-viewing of a blank scene. These measurements suggest a strong relationship between microsaccade generation and target detection during visual search. The long fixation durations during the blank scene exploration rule out the possibility that fixation duration is critical to target detection: the production of microsaccades was more significantly linked.

Average microsaccade magnitudes were higher in the free-viewing conditions (Table 2) than in the prolonged fixation conditions (Figure 3), lending further support to the idea that increased visual stimulation and/or task demands may result in increased microsaccade dynamics. We previously showed that precise fixation leads to decreases in microsaccade magnitudes (as well as microsaccade rates; Martinez-Conde et al., 2006), and that such decreases result in visual fading. Because subjects are not 'required' to fixate in the fixation periods that occur spontaneously during free-viewing, the reduction of microsaccade sizes associated with precise fixation may have not applied (or it may have applied less often), thus resulting in larger microsaccades than during prolonged fixation. An additional (non-exclusive) possibility is that some of the <1 deg saccades produced during free-viewing are not actual (involuntary) microsaccades but are rather voluntary or exploratory small saccades. But as discussed earlier, this potential caveat would also apply to the <1 deg saccades produced during visual fixation (which are defined by most current studies as microsaccades; Betta

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et al., 2007; Betta & Turatto, 2006; Engbert, 2006; Engbert & Kliegl, 2003a, 2003b, 2004; Engbert & Mergenthaler, 2006; Galfano et al., 2004; Laubrock et al., 2005; Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002, 2004, 2006; Rolfs et al., 2004, 2006; Troncoso, Macknik, & Martinez-Conde, 2008; Turatto et al., 2007; Valsecchi et al., 2007; Valsecchi & Turatto, 2007). Another potential explanation could be that relatively brief fixation periods (such as those during free-viewing) result in larger ocular instability (and thus larger microsaccades) than periods of prolonged fixation. To exclude this possibility, we compared the microsaccade magnitudes during the first several hundred milliseconds of the prolonged fixation trials to the microsaccade magnitudes found in the fixation periods during free-viewing. The difference in microsaccade magnitude for both types of trial remained mostly unaffected (data not shown).

Temporal interactions between saccades and microsaccades

If saccades and microsaccades share the same oculomotor bases, then microsaccade generation should affect the timing of saccade generation, and vice versa. Rolfs et al. (2006) found that microsaccades produced during fixation affect the timing of subsequent saccades. Here we determine the interactions for all the pair-wise combinations of saccades and microsaccades, both during fixation and free-viewing.

	Fixation	Free-viewing
N	35,882	123,992
Rate (N/sec)	0.8 ± 0.1	2.9 ± 0.1
Magnitude (deg)	0.55 ± 0.07	5.3 ± 0.3
Duration (ms)	13 ± 1	33 ± 1
Peak velocity (deg/s)	49 ± 4	217 ± 8

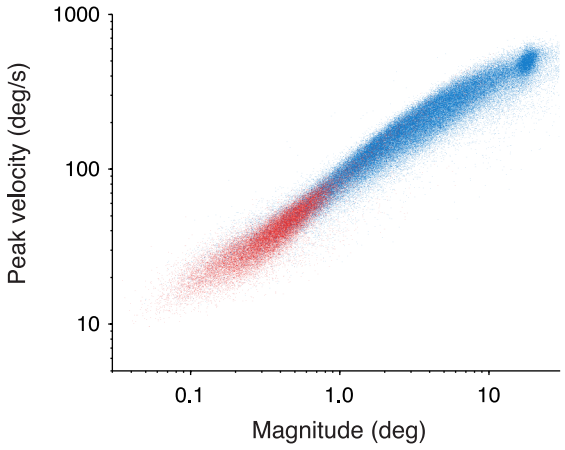

Figure 6. Microsaccades and saccades follow the same main sequence. Saccades and microsaccades recorded during free-viewing (blue) follow the same main sequence as those produced during the fixation conditions (red). Note that some of the blue dots are obscured by the superimposed red dots (i.e., when a red and a blue dot occupy the same location in the graph, the red dot is plotted over the blue dot). Microsaccade and saccade rates have been calculated taken into consideration the total time in each trial. N = 8 subjects.

Zuber and Stark (1965) first determined that microsaccades produced during fixation follow the saccadic main sequence, and thus proposed that there is a common generator for saccades and microsaccades. Figure 6 extends the range of the main sequence to include all saccades and microsaccades produced by the same subjects during visual fixation and free-viewing of the same images. Saccades and microsaccades produced during the fixation tasks are indicated in red. Saccades and microsaccades produced during the free-viewing tasks are indicated in blue. Both distributions follow the same main sequence, with the same slope.

Figure 7A shows that intersaccadic intervals are equivalent for all pair-wise combinations of saccades and microsaccades in free-viewing. That is, both saccades and microsaccades were more likely produced approximately 200 ms after a previous eye movement (which could itself be either a saccade or a microsaccade). In other words, the refractory periods between saccades and microsaccades are equivalent, irrespective of their sequential order. This observation is at odds with the idea of two different circuits for the generation of saccades and microsaccades. Saccades and microsaccades appear to share the same timing constraints, which supports the hypothesis of a common saccade–microsaccade generator. During fixation, the intervals between successive microsaccades are somewhat longer than during free-viewing. The reason may be that subjects try to hold their gaze steady during fixation, and so their microsaccade production may be—at least partly—suppressed (Martinez-Conde et al., 2006), resulting in longer intervals between successive microsaccades. Figure 7B plots the normalized distribution of intersaccadic intervals (for all saccades and microsaccades combined) according to experimental condition (all the fixation conditions are lumped together). In agreement with Figure 7A, intersaccadic intervals during the fixation conditions are slightly longer

Figure 7. Intersaccadic interval distributions. (A) Intersaccadic intervals follow similar distributions for all saccade–microsaccade combinations. The only variation between distributions occurs for intersaccadic intervals larger than ~200 ms. (B) Intersaccadic intervals follow similar distribution for all experimental conditions. (C) Intersaccadic interval distributions for individual conditions have been fit with ex-Gaussian curves (red). The blue dots show the histograms of the data used for the fits (same data as in (B)). (D) Variability of parameter estimations across experimental conditions. Only the exponential parameter (τ) varies significantly across conditions. (E) Parameter estimation as a function of saccade rate. There is a clear linear correlation between the exponential parameter (τ) and the rate of saccades.

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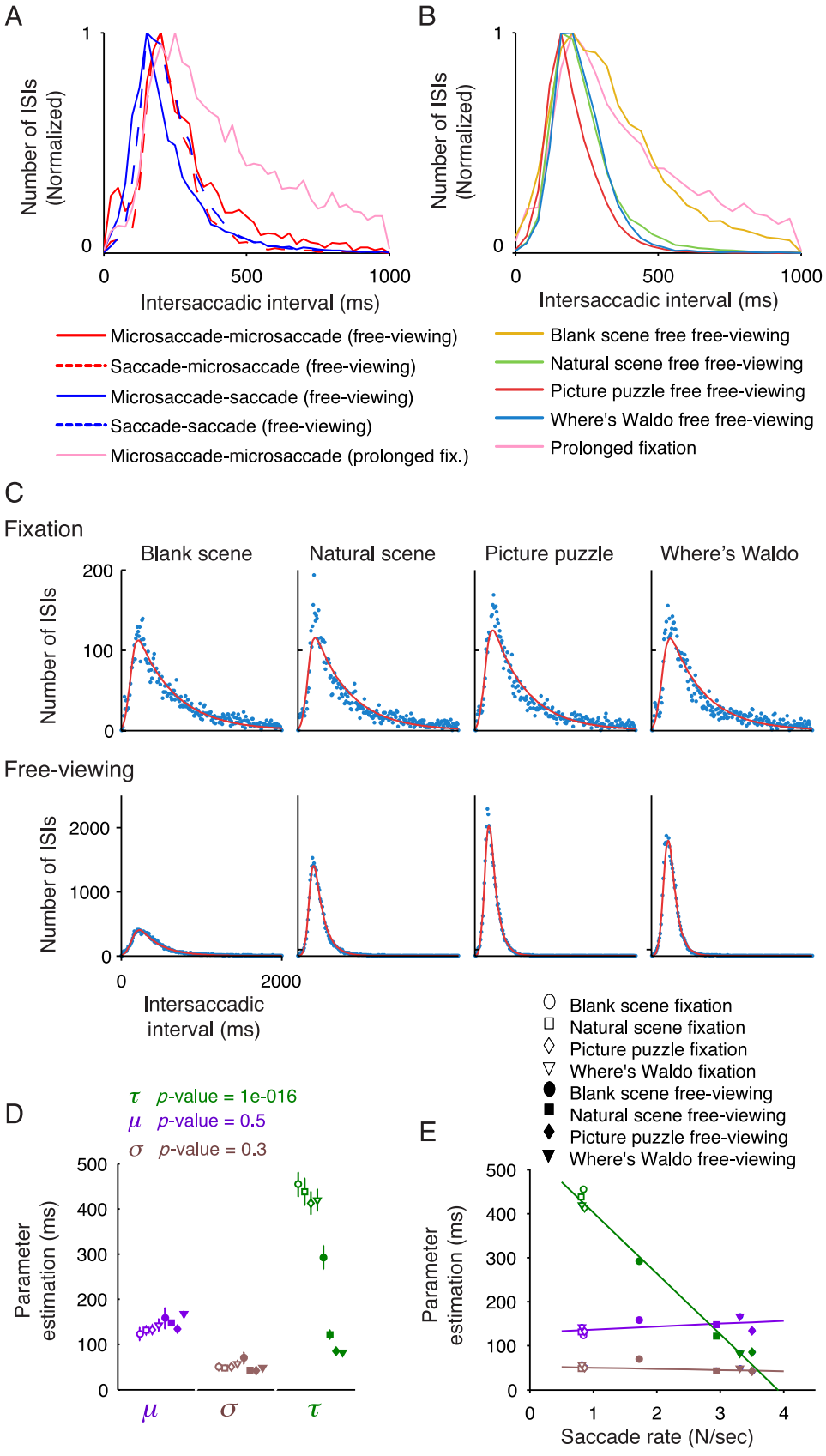

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than intersaccadic intervals during free-viewing. Most of the free-viewing conditions result in equivalent intersaccadic interval distributions. It is interesting to note that the free exploration of a blank scene results in very similar intersaccadic intervals to those produced during prolonged fixation. The underlying reason may be the relative scarcity of both saccades and microsaccades during blank-scene explorations, when compared to the other free-viewing conditions (see Tables 1 and 2). To sum up, the only variation between distributions occurs for intersaccadic intervals larger than ~200 ms, and this difference seems better related to the nature of the task than to dissimilarity in the generation of saccades vs. microsaccades. In Figure 7C, the distributions of intersaccadic intervals for individual conditions are fit with ex-Gaussian functions (see Methods section). Only the exponential parameter (τ) of the ex-Gaussian curve varied significantly across conditions (Figure 7D). This parameter indicates the rate of decay of the probability of a long intersaccadic interval. Figure 7E shows that the exponential parameter (τ) is linearly related to the saccade and/or microsaccade rate, as proposed earlier. The Gaussian component of the ex-Gaussian distribution is described by parameters μ (mean of the Gaussian distribution) and σ (width of the

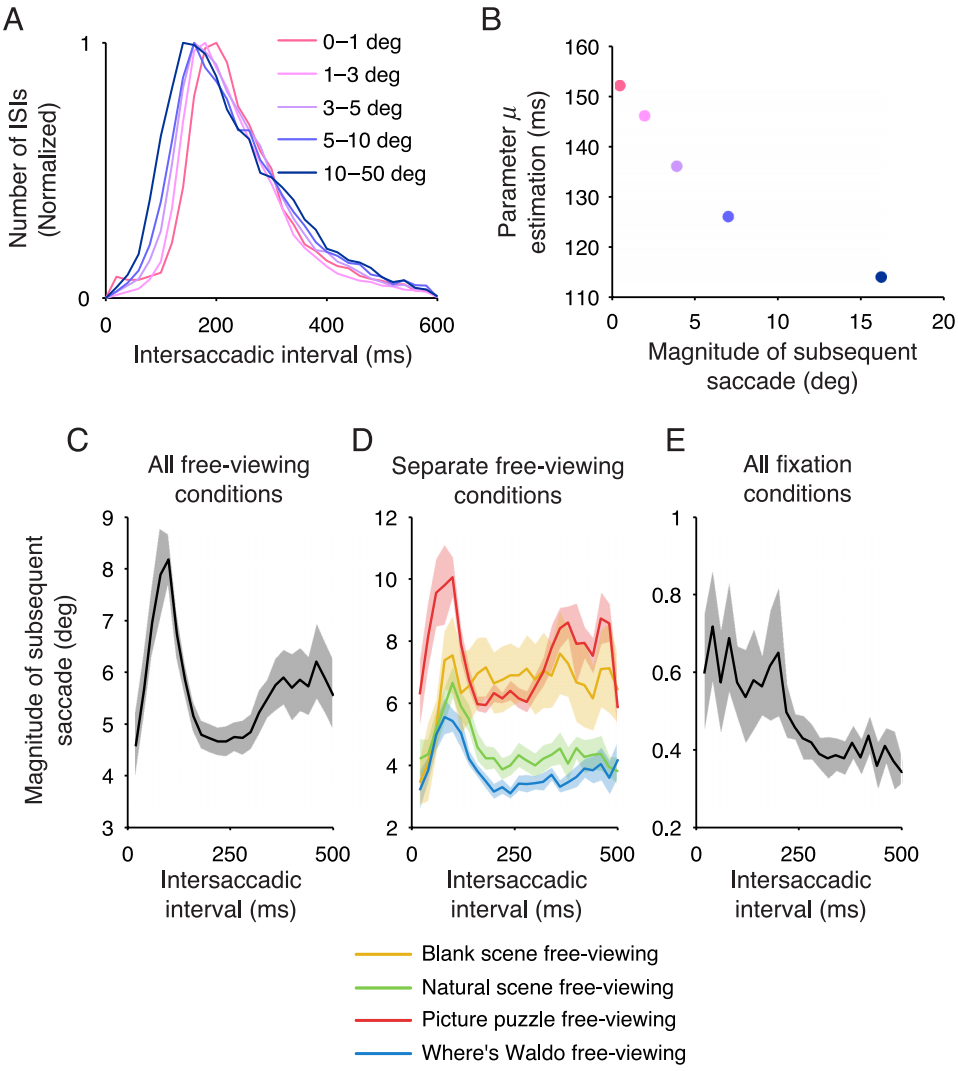

Figure 8. Relationship between intersaccadic intervals and the magnitude of subsequent saccades. (A) Distribution of intersaccadic intervals grouped by the magnitude of the subsequent saccade. Short intersaccadic intervals tend to be followed by large saccades. Conversely, long intersaccadic intervals tend to be followed by small saccades. (B) The parameter μ from the ex-Gaussian model fit to curves in (A) is parametrically related to the magnitude of the subsequent saccade. Note that microsaccades follow the same trend as large saccades. (C) Saccade magnitudes as a function of the duration of the preceding intersaccadic intervals. Short intersaccadic intervals are followed by large saccades. (D) Data from (C) now separated into individual free-viewing conditions. (E) Microsaccade magnitudes during fixation as a function of the duration of preceding intersaccadic intervals. Short intersaccadic intervals are followed by larger microsaccades. Conversely, long intersaccadic intervals are followed by smaller microsaccades.

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Gaussian distribution). Parameters μ and σ were not related to saccade and/or microsaccade rate, and they did not differ significantly across conditions.

Figure 8 relates the duration of intersaccadic intervals to the magnitude of the second (subsequent) saccade/microsaccade. Short intersaccadic intervals tend to be followed by large saccades; long intersaccadic intervals tend to be followed by small saccades/microsaccades (Figure 8A). Figure 8B shows that the magnitude of each subsequent saccade (in a saccade pair) is parametrically related to the parameter μ from the ex-Gaussian model fit to the data in Figure 8A. Note that microsaccades follow the same trend as large saccades. Figures 8C–8E show that the relationship between the duration of the intersaccadic intervals and the magnitude of the next saccade/microsaccade applies to both free-viewing conditions (as previously shown by Unema, Pannasch, Joos, & Velichkovsky, 2005, Figures 8C and 8D) and fixation conditions (Figure 8E), further supporting the hypothesis that saccades and microsaccades share a common generator.

Discussion

Microsaccades during free-viewing

Microsaccades are known to occur during prolonged visual fixation, but it has been a matter of controversy whether they are also produced during free-viewing. Here we set out to determine:

1. Whether microsaccades occur during free visual exploration and visual search,
2. Whether microsaccade generation varies with task, and
3. Whether saccades and microsaccades share equivalent spatiotemporal characteristics, which would argue in favor of a common saccade–microsaccade oculomotor generator.

In the late 1970s, Kowler and Steinman (Kowler & Steinman, 1980; Skavenski, Hansen, Steinman, & Winterson, 1979; Steinman & Collewijn, 1980) concluded that the generation of microsaccades was a laboratory artifact: i.e., that microsaccades did not occur in normal viewing conditions, but that they resulted from artificial laboratory conditions, in which subjects were forced to hold their gaze for very long periods of time, while their head was restrained (for instance, with a bite bar). Steinman, Haddad, Skavenski, and Wyman (1973) and Kowler and Steinman (1979, 1980) furthermore stated that microsaccades are not helpful in tasks requiring complex visual information processing, and thus are much less common during brief fixations interposed between large saccades (in activities such as reading or counting) than during prolonged fixation.

Contrary to these conclusions, we and others found in the last decade that microsaccades generate strong reliable firing in visual neurons during fixation, and also during the fixation periods in guided-viewing (Bair & O'Keefe, 1998; Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002, 2004). Moreover, microsaccades counteracted visual fading and filling-in and increased target's visibility in human subjects with both restrained and unrestrained heads (Martinez-Conde et al., 2006; Troncoso, Macknik, & Martinez-Conde, 2008). The dynamics of microsaccades with restrained versus unrestrained heads were equivalent, suggesting that microsaccades are generated with and without the presence of head movements (Martinez-Conde et al., 2006). One critical difference between these recent studies and the early microsaccade studies from the 1970s is the current standard use of objective microsaccade-detecting algorithms (developed within the last decade; Engbert & Kliegl, 2003b; Martinez-Conde et al., 2000). Current objective algorithms base microsaccade characterization on parameters derived from the distribution of involuntary saccades during visual fixation, rather than on arbitrary magnitude or velocity thresholds (as done in the earlier studies). Another possible confound in the earlier studies is that microsaccades were identified subjectively (i.e., picked by hand from the eye-position traces), which poses the potential difficulty of replication by other groups.

In a relatively recent example of the early subjective approach to microsaccade detection, Malinov, Epelboim, Herst, and Steinman (2000) identified microsaccades by hand, rather than by applying an objective algorithm. They also defined microsaccades arbitrarily (i.e., without previously quantifying the distribution of involuntary saccades during fixation), as saccades with magnitudes of <12 arcmin. This very stringent parameter is well below the average magnitude found and/or the upper microsaccade threshold used in recent microsaccade studies in humans and primates (Betta et al., 2007; Betta & Turatto, 2006; Engbert, 2006; Engbert & Kliegl, 2003a, 2003b, 2004; Engbert & Mergenthaler, 2006; Galfano et al., 2004; Laubrock et al., 2005; Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002, 2006; Rolfs et al., 2004, 2006; Snodderly, Kagan, & Gur, 2001; Turatto et al., 2007; Valsecchi et al., 2007; Valsecchi & Turatto, 2007), see also Martinez-Conde et al. (2004) for a review of human and primate microsaccade parameters. These limitations and potential confounds may help to explain why only 2 out of >3,000 total saccades recorded in Malinov et al.'s study in freely moving humans were classified as "microsaccades", in contradiction to the much higher number of microsaccades we find here. It is also important to keep in mind that microsaccade production during free-viewing depends on the nature of the visual stimulation and the task performed, as shown here. Thus free-viewing tasks that do not require the subject's attentive fixation may lead to reduced microsaccade production (such as in the free-viewing exploration of a blank scene; Figures 2 and 5, Table 2).

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To sum up, the role of microsaccades in free-viewing has remained controversial to date. However, the dynamics of microsaccades during free-viewing vs. fixation have not previously been objectively and systematically measured (i.e., with current microsaccade-detecting algorithms, previously unavailable). Our results show that microsaccades occur in the fixation periods that naturally take place during visual exploration and visual search (Figures 2, 4, and 5, Supplementary Movies 5–6). Moreover, microsaccade rates during the fixation periods in visual exploration/search were comparable to microsaccade rates during prolonged fixation (Table 2).

Our results also suggest that microsaccades and saccades have equivalent functional roles, both during prolonged fixation and during free-viewing. The spatiotemporal characteristics of microsaccades and saccades may reflect an optimal sampling method by which the brain discretely acquires visual information. Thus we put forward that the dichotomy between saccades and microsaccades proposed by previous studies is fundamentally arbitrary.

Saccades and microsaccades as an optimal sampling strategy

The dynamics of saccades and microsaccades may reflect an optimal strategy by which visual neurons discretely sample information from a scene. Visual exploration of a blank scene (in which visual information is absent by definition) resulted in low production of both saccades and microsaccades. The visual exploration/search of scenes that were rich with visual content resulted in much higher rates of saccades and microsaccades (Figure 4, Tables 1 and 2). As the cognitive demands of the task increased (Where's Waldo visual search vs. free visual exploration), microsaccade generation increased even further, especially in the regions with identified targets (Table 2, Figure 5, Supplementary Movies 5–6). These results are in agreement with physiological and modeling studies in the primate visual system, in which strong neural transients were observed in response to microsaccades (Donner & Hemilä, 2007; Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002), suggesting that microsaccades may improve the efficient sampling of fine spatial detail (Donner & Hemilä, 2007). Other studies suggest that V1 neurons produce stronger responses to transient stimuli than to drifting stimuli. Such neural transients may underlie the behavior of cortical neurons as coincidence detectors (Shelley, McLaughlin, Shapley, & Wielaard, 2002; Williams & Shapley, 2007). Moreover, neural transients to stimuli onsets and terminations (similar to those produced by microsaccades in the primate visual system; Martinez-Conde, 2006; Martinez-Conde et al., 2000, 2002) have been related to target visibility in visual masking paradigms (Macknik & Livingstone, 1998; Macknik & Martinez-Conde, 2004; Macknik, Martinez-Conde, & Haglund, 2000).

Gilchrist, Brown, and Findlay (1997) and Gilchrist, Brown, Findlay, and Clarke (1998) moreover observed that a patient who was unable to make eye movements (except for small-magnitude drifts) produced head-saccades of comparable characteristics to eye-saccades. Such head-saccades enabled the patient to read at normal speed and even perform complicated visuo-motor tasks, such as making a cup of tea, with no problems. The authors concluded that "saccadic movements, of the head or the eye, form the optimal sampling method for the brain" (Gilchrist et al., 1997, 1998). This type of discrete sampling is potentially optimal in other sensory systems as well. Sniffs during rodent olfaction also sample sensory information discretely every 200–300 ms and are thus comparable in their temporal dynamics to saccades (Uchida, Kepecs, & Mainen, 2006) and microsaccades in humans and primates. A similar mode of discrete sampling may also be at play when objects are recognized through tactile information, for instance if we sweep our fingertips over an object's surface with our eyes closed, or when blind individuals read Braille script.

Microsaccades in visual search and the role of attention

It has remained unknown whether microsaccade dynamics vary as a function of free-viewing task. Here we found microsaccades to be more prominent in conditions that involved complex/meaningful visual information (natural vs. blank scene, faces vs. non-faces) and increased cognitive/attentional demands (Where's Waldo vs. free visual exploration; Tables 1 and 2; Figures 4 and 5; Supplementary Movies 5–6). Conversely, the free exploration of a blank scene—where the visual content is null and the task demands are low—resulted in long fixation periods, but comparatively low microsaccade rates.

Previous studies have found that the spatial location of attention strongly influences the rate and/or the direction of microsaccades during visual fixation (Engbert, 2006; Engbert & Kliegl, 2003b; Galfano et al., 2004; Hafed & Clark, 2002; Rolfs et al., 2004, 2005). Thus increased microsaccade production due to increased attentional load may explain our current results, especially as microsaccade rates were highest in the regions of identified targets (Table 2).

Future research should determine how varied amounts of attentional load may impact microsaccade dynamics during visual search and other naturalistic tasks, and the potential physiological and perceptual consequences of such modulations. One possibility is that increased microsaccade production (perhaps due to increased attention) directly results in successful target detections (due to successive microsaccades repeatedly stimulating the receptive fields of visual neurons in the target area). Alternatively, the very first saccade or microsaccade to land on the target may be sufficient for detection, and the function of subsequent microsaccades may be to confirm

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the original identification of the target. Thus, future studies should also investigate the precise timing of microsaccade generation with regard to target detection and the interactions with attention.

A saccade–microsaccade continuum

A growing list of common characteristics to saccades and microsaccades supports the hypothesis of a shared oculomotor generator (Martinez-Conde et al., 2004; Rolfs et al., 2006, 2008; Zuber & Stark, 1965). Most studies to date have focused on the descriptive parameters of saccades and microsaccades (magnitude, duration, peak velocity–magnitude relationship). Here we hypothesized that, if saccades and microsaccades share the same oculomotor bases, microsaccade generation should affect saccade generation, and vice versa. Our results indicate that the spatiotemporal parameters of saccades and microsaccades are equivalent (Figures 6, 7, and 8), providing further evidence for the common generator hypothesis. In agreement with this idea, Van Gisbergen and colleagues found that the activity of burst neurons in the abducens nucleus and nearby pontomedullary reticular formation is similar for saccades and microsaccades (Van Gisbergen & Robinson, 1977; Van Gisbergen, Robinson, & Gielen, 1981).

To date, the study of microsaccades during free-viewing has faced a two-pronged challenge:

1. If fixation periods are defined as saccade-free periods, it follows that fixational microsaccades are not part of fixation; a contradiction in terms.
2. But if microsaccades are indeed a type of fixational eye movement (Ditchburn & Ginsborg, 1952, 1953; Ratliff & Riggs, 1950, see Martinez-Conde et al., 2004 for a review), then they must be included within the fixation periods.

Our results suggest that such difficulty is fundamentally semantic: we propose that there is a microsaccade–saccade continuum, and that visual information is discretely sampled with all saccades, large and small (including microsaccades). The fact that there is a minimal intersaccadic interval (i.e., a refractory period) preceding saccades and microsaccades, and that this interval is similar for all pair-wise combinations of saccades and microsaccades, argues strongly against a very strict divide between the neural mechanisms responsible for the generation of saccades and microsaccades.

Practical implications for future research

Commercially available algorithms for saccade detection are often used to separate saccades from fixation periods during free-viewing tasks (such as visual exploration, visual search, reading, etc.). The thresholds used for such saccade detection can be quite arbitrary. For instance, the EyeLink II manual (SR Research, 2006) recommends a velocity threshold of 22 deg/s for "smooth pursuit and psychophysical research" and a velocity threshold of 30 deg/s for "reading and cognitive research". The present results show that the use of such thresholds for the identification of saccades and/or microsaccades is problematic. Here we would like to emphasize two practical points:

1. Microsaccade characterization during free-viewing should be based on parameters obtained from microsaccade distributions during prolonged fixation, ideally collected from the same subjects (and necessarily from the same species, i.e., primates vs. humans).
2. Future studies investigating microsaccades and/or fixation periods during free-viewing should report the precise thresholds used for the classification of saccades/microsaccades/fixation periods, rather than simply state the name of the commercial software package used to characterize eye movements.

Finally, because of the microsaccade–saccade continuum proposed above, we recommend that future studies of visual exploration/search employ saccade-detecting algorithms that allow the identification and inclusion of microsaccades (rather than using thresholds that arbitrarily exclude the potential contributions of microsaccades/small saccades).

Conclusions

We found that microsaccades occur during visual exploration and visual search, and that their specific dynamics vary as a function of visual stimulation and viewing task, with more challenging tasks resulting in higher microsaccade production. Saccades and microsaccades had comparable spatiotemporal characteristics, including equivalent intersaccadic intervals between all pair-wise combinations of saccades and microsaccades. We propose that the dichotomy between saccades and microsaccades suggested by previous studies is fundamentally arbitrary. Rather, our results indicate a microsaccade–saccade continuum and suggest that saccades and microsaccades are generated by common brain circuits. The spatiotemporal characteristics of saccades and microsaccades may reflect an optimal sampling method by which the brain discretely acquires visual information.

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References

Adams, M. (Ed.). (2006a). *Life picture puzzle: Can you spot the differences?* (vol. 6(2)). Life Books.

Adams, M. (Ed.). (2006b). *Life picture puzzle: Can you spot the differences?* (vol. 7(2)). Life Books.

Adams, M. (Ed.). (2006c). *Life picture puzzle: Can you spot the differences?* (vol. 7(5)). Life Books.

Bair, W., & O'Keefe, L. P. (1998). The influence of fixational eye movements on the response of neurons in area MT of the macaque. *Visual Neuroscience, 15,* 779–786. [PubMed]

Betta, E., Galfano, G., & Turatto, M. (2007). Microsaccadic response during inhibition of return in a target–target paradigm. *Vision Research, 47,* 428–436. [PubMed]

Betta, E., & Turatto, M. (2006). Are you ready? I can tell by looking at your microsaccades. *Neuroreport, 17,* 1001–1004. [PubMed]

Ditchburn, R. W., & Ginsborg, B. L. (1952). Vision with a stabilized retinal image. *Nature, 170,* 36–37. [PubMed]

Ditchburn, R. W., & Ginsborg, B. L. (1953). Involuntary eye movements during fixation. *The Journal of Physiology, 119,* 1–17. [PubMed] [Article]

Donner, K., & Hemilä, S. (2007). Modelling the effect of microsaccades on retinal responses to stationary contrast patterns. *Vision Research, 47,* 1166–1177. [PubMed]

Engbert, R. (2006). Microsaccades: A microcosm for research on oculomotor control, attention, and visual perception. *Progress in Brain Research, 154,* 177–192. [PubMed]

Engbert, R., & Kliegl, R. (2003a). Binocular coordination in microsaccades. In R. R. J. Hyona & H. Deubel (Eds.), *The mind's eyes: Cognitive and applied aspects of eye movements* (pp. 103–117). Oxford, UK: Elsevier.

Engbert, R., & Kliegl, R. (2003b). Microsaccades uncover the orientation of covert attention. *Vision Research, 43,* 1035–1045. [PubMed]

Engbert, R., & Kliegl, R. (2004). Microsaccades keep the eyes' balance during fixation. *Psychological Science, 15,* 431–436. [PubMed]

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences of the United States of America, 103,* 7192–7197. [PubMed] [Article]

Galfano, G., Betta, E., & Turatto, M. (2004). Inhibition of return in microsaccades. *Experimental Brain Research, 159,* 400–404. [PubMed]

Gilchrist, I. D., Brown, V., & Findlay, J. M. (1997). Saccades without eye movements. *Nature, 390,* 130–131. [PubMed]

Gilchrist, I. D., Brown, V., Findlay, J. M., & Clarke, M. P. (1998). Using the eye-movement system to control the head. *Proceedings of the Royal Society B: Biological Sciences, 265,* 1831–1836. [PubMed] [Article]

Hafed, Z. M., & Clark, J. J. (2002). Microsaccades as an overt measure of covert attention shifts. *Vision Research, 42,* 2533–2545. [PubMed]

Handford, M. (2007a). *Where's Waldo now?* Cambridge, MA: Candlewick Press.

Handford, M. (2007b). *Where's Waldo? The wonder book.* Cambridge, MA: Candlewick Press.

Handford, M. (2007c). *Where's Waldo?* Cambridge, MA: Candlewick Press.

Hockley, W. E. (1984). Analysis of response time distributions in the study of cognitive processes. *Journal of Experimental Psychology: Learning, Memory, & Cognition, 10,* 598–615.

Juhel, J. (1993). Should we take the shape of reaction time distributions into account when studying the relationship between RT and psychometric intelligence? *Personality & Individual Differences, 15,* 357–360.

Kowler, E., & Steinman, R. M. (1979). Miniature saccades: Eye movements that do not count. *Vision Research, 19,* 105–108. [PubMed]

Kowler, E., & Steinman, R. M. (1980). Small saccades serve no useful purpose: Reply to a letter by R. W. Ditchburn. *Vision Research, 20,* 273–276. [PubMed]

Laubrock, J., Engbert, R., & Kliegl, R. (2005). Microsaccade dynamics during covert attention. *Vision Research, 45,* 721–730. [PubMed]

Lord, M. P. (1951). Measurement of binocular eye movements of subjects in the sitting position. *British*

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Journal of Ophthalmology, 35, 21–30. [PubMed] [Article]

Macknik, S. L., & Livingstone, M. S. (1998). Neuronal correlates of visibility and invisibility in the primate visual system. *Nature Neuroscience, 1,* 144–149. [PubMed]

Macknik, S. L., & Martinez-Conde, S. (2004). The spatial and temporal effects of lateral inhibitory networks and their relevance to the visibility of spatiotemporal edges. *Neurocomputing, 58–60,* 775–782.

Macknik, S. L., Martinez-Conde, S., & Haglund, M. M. (2000). The role of spatiotemporal edges in visibility and visual masking. *Proceedings of the National Academy of Sciences of the United States of America, 97,* 7556–7560. [PubMed] [Article]

Malinov, I. V., Epelboim, J., Herst, A. N., & Steinman, R. M. (2000). Characteristics of saccades and vergence in two kinds of sequential looking tasks. *Vision Research, 40,* 2083–2090. [PubMed]

Martinez-Conde, S. (2006). Fixational eye movements in normal and pathological vision. *Progress in Brain Research, 154,* 151–176. [PubMed]

Martinez-Conde, S., & Macknik, S. L. (2008). Fixational eye movements across vertebrates: Comparative dynamics, physiology and perception. *Journal of Vision, 8,* 1–16.

Martinez-Conde, S., & Macknik, S. L. (2007). Windows on the mind. *Scientific American, 297,* 56–63. [PubMed]

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2000). Microsaccadic eye movements and firing of single cells in the striate cortex of macaque monkeys. *Nature Neuroscience, 3,* 251–258. [PubMed]

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2002). The function of bursts of spikes during visual fixation in the awake primate lateral geniculate nucleus and primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America, 99,* 13920–13925. [PubMed] [Article]

Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2004). The role of fixational eye movements in visual perception. *Nature Reviews, Neuroscience, 5,* 229–240. [PubMed]

Martinez-Conde, S., Macknik, S. L., Troncoso, X. G., & Dyar, T. A. (2006). Microsaccades counteract visual fading during fixation. *Neuron, 49,* 297–305. [PubMed] [Article]

Møller, F., Laursen, M. L., Tygesen, J., & Sjølie, A. K. (2002). Binocular quantification and characterization of microsaccades. *Graefe's Archive for Clinical and Experimental Ophthalmology, 240,* 765–770. [PubMed]

Ratliff, F., & Riggs, L. A. (1950). Involuntary motions of the eye during monocular fixation. *Journal of Experimental Psychology, 40,* 687–701. [PubMed]

Riggs, L. A., & Ratliff, F. (1952). The effects of counteracting the normal movements of the eye. *Journal of the Optical Society of America, 42,* 872–873.

Rohrer, D., & Wixted, J. T. (1994). An analysis of latency and interresponse time in free recall. *Memory & Cognition, 22,* 511–524. [PubMed]

Rolfs, M., Engbert, R., & Kliegl, R. (2004). Microsaccade orientation supports attentional enhancement opposite a peripheral cue: Commentary on Tse, Sheinberg, and Logothetis (2003). *Psychological Science, 15,* 705–707. [PubMed]

Rolfs, M., Engbert, R., & Kliegl, R. (2005). Crossmodal coupling of oculomotor control and spatial attention in vision and audition. *Experimental Brain Research, 166,* 427–439. [PubMed]

Rolfs, M., Kliegl, R., & Engbert, R. (2008). Toward a model of microsaccade generation: The case of microsaccadic inhibition. *Journal of Vision, 8*(11):5, 1–23, http://journalofvision.org/8/11/5/, doi:10.1167/8.11.5. [PubMed] [Article]

Rolfs, M., Laubrock, J., & Kliegl, R. (2006). Shortening and prolongation of saccade latencies following microsaccades. *Experimental Brain Research, 169,* 369–376. [PubMed]

Shelley, M., McLaughlin, D., Shapley, R., & Wielaard, J. (2002). States of high conductance in a large-scale model of the visual cortex. *Journal of Computational Neuroscience, 13,* 93–109. [PubMed]

Skavenski, A. A., Hansen, R. M., Steinman, R. M., & Winterson, B. J. (1979). Quality of retinal image stabilization during small natural and artificial body rotations in man. *Vision Research, 19,* 675–683. [PubMed]

Snodderly, D. M., Kagan, I., & Gur, M. (2001). Selective activation of visual cortex neurons by fixational eye movements: Implications for neural coding. *Visual Neuroscience, 18,* 259–277. [PubMed]

SR Research (2006). EyeLink® II User Manual. Version 2.12. *SR. Research*, Mississauga, Canada.

Steinman, R. M., & Collewijn, H. (1980). Binocular retinal image motion during active head rotation. *Vision Research, 20,* 415–429. [PubMed]

Steinman, R. M., Haddad, G. M., Skavenski, A. A., & Wyman, D. (1973). Miniature eye movement. *Science, 181,* 810–819. [PubMed]

Troncoso, X., Macknik, S. L., & Martinez-Conde, S. (2008). Microsaccades counteract perceptual filling-in. *Journal of Vision, 8,* 1–9.

Troncoso, X., Macknik, S. L., Otero-Millan, J., & Martinez-Conde, S. (2008). Microsaccades drive

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illusory motion in the Enigma illusion. *Proceedings of the National Academy of Sciences of the United States of America, 105,* 16033–16038. [PubMed]

Turatto, M., Valsecchi, M., Tamè, L., & Betta, E. (2007). Microsaccades distinguish between global and local visual processing. *Neuroreport, 18,* 1015–1018. [PubMed]

Uchida, N., Kepecs, A., & Mainen, Z. F. (2006). Seeing at a glance, smelling in a whiff: Rapid forms of perceptual decision making. *Nature Reviews, Neuroscience, 7,* 485–491. [PubMed]

Unema, P. J., Pannasch, S., Joos, M., & Velichkovsky, B. M. (2005). Time course of information processing during scene perception: The relationship between saccade amplitude and fixation duration. *Visual Cognition, 12,* 473–494.

Valsecchi, M., Betta, E., & Turatto, M. (2007). Visual oddballs induce prolonged microsaccadic inhibition. *Experimental Brain Research, 177,* 196–208. [PubMed]

Valsecchi, M., & Turatto, M. (2007). Microsaccadic response to visual events that are invisible to the superior colliculus. *Behavioral Neuroscience, 121,* 786–793. [PubMed]

Van Gisbergen, J. A., Robinson, D. A., & Gielen, S. (1981). A quantitative analysis of generation of saccadic eye movements by burst neurons. *Journal of Neurophysiology, 45,* 417–442. [PubMed]

Van Gisbergen, J. A. M., & Robinson, D. A. (1977). Generation of micro and macrosaccades by burst neurons in the monkey. In R. Baker & A. Berthoz (Eds.), *Control of gaze by brain stem neurons*. New York: Elsevier/North-Holland.

Van Zandt, T. (2000). How to fit a response time distribution. *Psychonomic Bulletin & Review, 7,* 424–465. [PubMed]

Williams, P. E., & Shapley, R. M. (2007). A dynamic nonlinearity and spatial phase specificity in macaque V1 neurons. *Journal of Neuroscience, 27,* 5706–5718. [PubMed] [Article]

Yarbus, A. L. (1967). Eye movements and vision. In B. Haigh (Ed.). New York: Plenum Press.

Zuber, B. L., & Stark, L. (1965). Microsaccades and the velocity–amplitude relationship for saccadic eye movements. *Science, 150,* 1459–1460. [PubMed]

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